10-2-2006

Effects of Living Mulches on Predator Abundance and Sentinel Prey in a Corn–Soybean–Forage Rotation

Jarrad R. Prasifka
United States Department of Agriculture, Jarrad.Prasifka@ars.usda.gov

Nicholas Schmidt
United States Department of Agriculture

Keith A. Kohler
United States Department of Agriculture, keith.kohler@ars.usda.gov

Matthew E. O'Neal
Iowa State University, oneal@iastate.edu

Richard L. Hellmich
United States Department of Agriculture, richard.hellmich@ars.usda.gov

Effects of Living Mulches on Predator Abundance and Sentinel Prey in a Corn–Soybean–Forage Rotation

Author(s): J. R. Prasifka, N. P. Schmidt, K. A. Kohler, M. E. O'neal, R. L. Hellmich, and J. W. Singer
Source: Environmental Entomology, 35(5):1423-1431. 2006.
Published By: Entomological Society of America
DOI: http://dx.doi.org/10.1603/0046-225X(2006)35[1423:EOLMOP]2.0.CO;2
URL: http://www.bioone.org/doi/full/10.1603/0046-225X%282006%2935%5B1423%3AEOLMOP%5D2.0.CO%3B2

Effects of Living Mulches on Predator Abundance and Sentinel Prey in a Corn–Soybean–Forage Rotation

J. R. PRASIFKA,[1,2] N. P. SCHMIDT,[3] K. A. KOHLER,[4] M. E. O'NEAL,[3] R. L. HELLMICH,[1] AND J. W. SINGER[4]

Environ. Entomol. 35(5): 1423–1431 (2006)

ABSTRACT Living mulches are cover crops grown concurrently within main crops for their benefits to weed control and soil quality. Because living mulches increase the diversity of vegetation in agricultural systems, they may impact the abundance or effectiveness of natural enemies. To examine the effects of living mulches on epigeal predators, arthropod abundance and feeding were examined in a rotation of corn (*Zea mays* L.), soybean (*Glycine max* L. Merr.), and forage crops in 2004 and 2005. Compared with a no-mulch control, the presence of alfalfa (*Medicago sativa* L.) and kura clover (*Trifolium ambiguum* M. Bieb.) mulches in corn and soybean increased predator abundance and consumption of European corn borer (*Ostrinia nubilalis* Hübner; Lepidoptera: Crambidae) pupae used as sentinel prey. A complementary effect of increased predation caused by corn and soybean was found when both annual crops with living mulches were compared with mulches grown alone. Positive correlations between the percentage of *O. nubilalis* pupae preyed on and ground beetle (Coleoptera: Carabidae) abundance suggest carabids contributed to the differences in predation. In 2005, fewer beetles correlated with consumption of *O. nubilalis* pupae [*Poecilus chalcites* (Say) and *Scarites quadriceps* Chaudior] were collected, and living mulch impacts on predation were less frequent. Both changes could be related to delayed herbicidal suppression of the living mulches in 2005, which seemed to homogenize predator community composition among the corn, soybean, and forage plots. Although living mulches alone may not provide sufficient pest suppression, their potential to enhance biological control should be considered along with their other agronomic benefits.

KEY WORDS ground cover, predation, pitfall traps, community composition, *Harpalus pensylvanicus* (DeGeer)

Living mulches are plants grown within a main crop primarily to reduce erosion, suppress weeds, and recycle excess nutrients (Hartwig and Ammon 2002). Unlike other types of cover crops, living mulches are not killed before planting of the main crop, but are retained as living ground covers. While they may enhance the sustainability of cropping systems, living mulches often require mechanical or chemical suppression to prevent competition with the main crop (Brandsæter et al. 1998, Tharp and Kells 2001, Affeldt et al. 2004), which can be exacerbated by water or nitrogen limitations (Echtenkamp and Moomaw 1989, Duiker and Hartwig 2004). However, legumes used as living mulches may reduce fertilizer requirements by providing fixed nitrogen to the main crop (Brophy et al. 1987, Mallarino et al. 1990), and yields may be greater than or equal to those produced using conventional crop production methods (Enache and Ilnicki 1990, Ilnicki and Enache 1992, Costello 1994). Because the addition of a living mulch also increases the diversity of vegetation in an agricultural system, changes in the abundance or composition of arthropod pests and natural enemies are also expected (Risch et al. 1983, Andow 1991).

Several studies support the hypothesis that the use of living mulches reduces pest populations. In particular, aphid densities are frequently lower in crops incorporating living mulches (Costello 1994, Bigler et al. 1995a, Costello and Altieri 1995, Vidal 1997, Hooks et al. 1998, Frank and Liburd 2005). Lepidopteran pest levels (Bigler et al. 1995a, Hooks and Johnson 2004) or damage (Brandsæter et al. 1998) also may be reduced in crops grown with a living mulch. However, efforts should be made to determine whether a mulch provides the right type of diversity to the main crop; the use of living mulches may be problematic if specialist natural enemies (i.e., host-specific parasitoids) are impaired (Costello and Altieri 1995) or pest problems are exacerbated for other reasons (Hummel et al. 2002). Because previous studies on the impact of living mulches on arthropod pest management have focused

Mention of a proprietary product does not constitute an endorsement or a recommendation by Iowa State University or USDA for its use.

[1] USDA–ARS, Corn Insects and Crop Genetics Research Unit, Genetics Laboratory c/o Insectary, Iowa State University, Ames, IA 50011.

[2] Corresponding author, e-mail: prasifka@iastate.edu.

[3] Department of Entomology, Iowa State University, Ames, IA 50011.

[4] USDA–ARS, National Soil Tilth Laboratory, Ames, IA 50011.

on vegetable production systems, more research is required to determine if living mulches can be successfully integrated into the most widely grown annual crops.

When the addition of a living mulch to a cropping system succeeds in reducing pest populations, cause-and-effect relationships are confounded for at least two reasons. First, reduced pest populations may arise from more than one proximate cause. Mulches can impair the ability of some herbivores to find host plants (the resource concentration hypothesis; Root 1973, Andow 1991), reducing herbivore density directly by lowering colonization rates (Costello 1995, Finch and Kienegger 1997, Vidal 1997). Living mulches also may increase natural enemy abundance, lowering pest levels indirectly by improving biological control (the enemies hypothesis; Root 1973, Sheehan 1986, Russell 1989). In particular, predators including spiders (Bigler et al. 1995b, Hooks and Johnson 2004), ground-dwelling beetles (Bigler et al. 1995b), and hover flies (Vidal 1997) seem to be positively impacted by the addition of living mulches. Second, attempts to correlate improved pest suppression with natural enemy abundance or efficacy (e.g., percent predation or parasitism) are complicated because both may be related to numerical or functional responses (Holling 1961). That is, predators may simply be more abundant or more effective at higher pest densities (Vidal 1997, Hooks et al. 1998), although even inverse density dependence seems possible in some situations (Vidal 1997).

In this study, living mulches in a 3-yr crop rotation were examined for their potential to enhance biological control with attempts made to reduce the confounding factors of herbivore colonization and density dependence. Nitrogen-fixing mulches of alfalfa (*Medicago sativa* L.) and kura clover (*Trifolium ambiguum* M. Bieb.) were established and either partially suppressed (mechanically or chemically) within main crops of corn (*Zea mays* L.) and soybean (*Glycine max* L. Merr.), or grown alone as forage crops. To address the hypothesis that living mulches can impact biological control in corn and soybean, the study objectives were to (1) determine if living mulches changed the abundance of epigeal (ground-dwelling) predators or (2) affected consumption of sentinel prey and (3) test whether the percentage of prey fed on was positively correlated with the abundance of one or more groups of predators.

Materials and Methods

The possible effects of alfalfa and kura clover on predator abundance and feeding were assessed during 2004 and 2005 as part of a larger experiment examining the agronomic potential of nine perennial (single and multiple species) living mulches integrated into a corn–soybean–forage crop rotation. In this rotation, the forage component consisted of species in the living mulches grown without either annual crop. Alfalfa and kura clover were selected as representatives of living mulches providing high and intermediate levels of ground cover, respectively. The research was located at a site 10 km west of Ames, IA (42°01′ N, 93°45′ W), with predominantly Nicollet loam soil. Before 2002, corn and soybean were annually rotated at the site. In 2002, spring oat (*Avena sativa* L.) was planted in April and harvested in July.

Establishment and Maintenance of Experimental Plots. After a brief fallow period, plots were established in a randomized complete block design with split-plots and four replications. Whole plots were assigned to corn, soybean, or forage crops in blocks separated by at least 9.1 m. Living mulch split-plots (3.8 by 18.3 m) were planted in August 2002 with a no-tillage grain drill in 0.20-m rows, with alfalfa ('ABI ZG9834') and kura clover ('Rhizo') seeded at 16.8 and 9.0 kg/ha, respectively. In 2003, living mulches were allowed to establish. Stand losses of kura clover required reseeding in August, and forages were harvested to 6 cm height four times (monthly from June to September). After the first and third cuttings, phosphorus and potassium were applied at rates based on soil samples collected in the spring (Voss et al. 2002). In 2004, harvests of forage plots occurred monthly from May though August, with phosphorus and potassium applied as in 2003.

Although the control (no living mulch) within the forage (no annual crop) whole plots would logically be left fallow, alfalfa ('WL711') was drilled into these split-plots, which were not used to characterize predator abundance, community composition, or feeding as described below. While the lack of a mulch-free split-plot in the forage whole plots produced an unbalanced experimental design, any comparisons to idle, cultivated land were not considered relevant to study objectives.

Corn whole plots were planted with Dekalb 'DKC53–33' on 16 April 2004 (86,500 seeds/ha, 0.76-m rows). To promote growth of corn, living mulch split-plots received a 0.25-m-wide herbicide band application over the seed row (glyphosate, 1.41 kg [AI]/ha; S-metolachlor, 2.24 kg [AI]/ha tank-mixed in 168 liters/ha of water) on 23 April. Subsequent control of the mulches was accomplished mechanically with a rolling stalk chopper (cutting between rows to 15 cm height monthly from April through June) and chemically (glyphosate band application in May). Control split-plots were maintained weed-free with glyphosate and hand weeding as necessary. Split-plots received nitrogen side-dressed as a 32% urea-NH_4NO_3 solution using a point-injection applicator at rates based on soil samples (Blackmer et al. 1989).

Soybean whole plots were planted with Asgrow 'AG2107' on 21 May 2004 (445,000 seeds/ha, 0.76-m rows). Before planting, in-row control of mulches in soybean had been achieved with an herbicide band treatment (23 April, as in corn) and a harvest of mulch between rows (20 May). Additional control of the living mulches was performed in June, when mulch between rows was cut with the stalk chopper and in-row mulch growth was suppressed with a glyphosate band application. Control split-plots were maintained weed-free with glyphosate and hand weeding.

Plot maintenance in 2005 was similar to the previous year with two exceptions. First, to simulate a corn–soybean–forage crop rotation, the annual crops were moved so that corn was planted into the plots used for forage in 2004; correspondingly, in plots where corn was grown the previous year, soybean was planted. Also, although planting dates in the corn (15 April) and soybean (24 May) whole plots were similar to the previous year, both of the glyphosate band applications were delayed ~5 wk relative to 2004.

Predator Abundance and Composition. Pitfall traps were used to estimate the abundance of arthropod predators. Within each split-plot, two pitfall traps were used to sample ground-dwelling arthropods. Traps were placed into holes made using a golf cup cutter in the center row (third of five) of living mulch split-plots, inset 6 m from opposite ends. Pitfall traps consisted of cups (1,000 ml, GC33TH; Sweetheart Cup Co., Owings Mills, MD) with lids, placed into the soil just below ground level. For 72 h once monthly from June through September, pitfall traps were activated by removal of the lids. Trap contents were collected daily because the cups contained no killing fluid. Although using pitfall traps is inappropriate when absolute measures of population density are required, they were considered suitable in this case because all plots were sampled concurrently, and only relative comparisons were necessary.

Samples were stored frozen until their contents could be identified. Some arthropod groups more accurately characterized as omnivores were collected from pitfall traps and included as predators if known to feed on living or dead arthropods. Predators were sorted into groups and identified to order (all Arachnida) or family (most Insecta). However, ground beetles (Coleoptera: Carabidae) were identified to species level, with voucher specimens deposited in the Iowa State University Insect Collection.

Feeding on Sentinel Prey. At the onset of pitfall trapping, small cages used to measure predation were placed in the plots. Cages were cylindrical, 9 cm high and 14.5 cm in diameter, each constructed from a strip of wire mesh (1.3 cm mesh, 19-gauge hardware cloth) whose ends were fastened together using pop-rivets and washers. The mesh size selected was intended to exclude vertebrates from cages while allowing ground-dwelling invertebrates to enter and leave cages. Two cages per split-plot were placed within 1 m of pitfall trap locations (in the center row, 6 m from the ends) and pushed 2.5 cm into the soil surface to prevent movement of the cages. Cage covers (15 cm diameter petri dish tops, 351058; BD Biosciences, Bedford, MA) were also placed tightly over the tops to reduce possible disturbance by vertebrate animals or rainfall.

Within 1 wk of each period of pitfall trapping (June through September), sentinel prey were placed into the cages. Prey consisted of laboratory-reared European corn borer (*Ostrinia nubilalis* Hübner) pupae that had been frozen (24 h at −16°C) and hot-glued onto cards (10 pupae on each 7.6 by 12.7-cm piece) of sandpaper (60 grade, 346U; 3M Co., St. Paul, MN). After 72 h in the plots, cards were placed into sealable plastic bags and stored frozen until they could be examined. Each card was viewed under a dissecting microscope, and individual pupae were categorized as intact (no evidence of feeding), preyed on (some pupal material removed), or missing (absent with no material remaining).

Statistical Analysis. All analyses were performed using SAS statistical software (SAS Institute 1999), using specific procedures as indicated in capital letters. Preliminary tests on natural enemy abundance and predation data examined the effects of crop type (whole plots) and living mulches (split-plots) using a split-plot model with time treated as a repeated measure (PROC MIXED). However, significant time × crop and time × mulch interactions suggested that data would be more appropriately examined using separate analyses for each sample period.

Accordingly, pitfall trap data were analyzed with separate split-plot analyses of variance at each date (PROC MIXED). Frequency distributions of total predator abundance were skewed. Consequently, the dependant variable used for analysis was $\log_{10}$ (predator abundance + 1), with predator abundance calculated as the sum of all predatory taxa collected. Explanatory variables in the mixed model included fixed effects of crop type, mulch type, crop × mulch interaction, and random effects (including interactions) related to replicates (blocks). *F*-tests for the fixed effects were considered an initial step of testing, which was followed by a series of three CONTRAST statements. At each sample period, contrasts were used to test for differences between both living mulches (alfalfa and kura clover combined) and the no-mulch control in (1) corn and (2) soybean. An additional contrast compared both living mulches in the annual crops (corn and soybean combined) to both mulches (3) in the forage main plots. These contrasts helped account for the unbalanced nature of the experiment (i.e., the lack of a mulch-free split-plot in the forage whole plots) and provide supplementary tests when crop × mulch interactions occurred. The data from the sentinel prey experiment were analyzed in the same manner as predator abundance data with one exception. The dependent variable, percent predation, for each plot was calculated as the number of pupae preyed on divided by the sum of the number preyed on and intact. The angular (arcsine-square root) transformation commonly applied to percent data was not used because the percent predation values were most often not close to the extremes (0 or 100%), and analyses using the transformation indicated it would have little impact on the results.

To test whether significant differences in consumption of sentinel prey were related to the abundance of any particular predator taxa, simple correlation was used. For each instance that a contrast statement indicated an effect of crop or mulch on percent predation values, scatter plots of the corresponding percent predation and $\log_{10}(x + 1)$ predator abundance data were examined. If positive correlations to percent predation appeared to be present for any groups (in-

Table 1. Relative abundance (%) of common predator taxa in whole plots by year and crop type, 2004–2005

Taxon	Year and crop type					
	2004			2005		
	Corn[a] (n = 310)	Soybean (n = 244)	Forage (n = 288)	Corn (n = 454)	Soybean (n = 462)	Forage (n = 299)
Carabid adults	55	61	28	60	56	41
Poecilus chalcites (Say)	13	11	2	2	2	1
Scarites quadriceps Chaudior	12	14	<1	4	6	3
Pterostichus permundus (Say)	10	14	1	8	14	4
Harpalus pensylvanicus (DeGeer)	7	7	10	24	19	13
Carabid larvae	16	5	3	0	0	0
Opiliones	5	9	32	26	31	35
Araneae	16	8	18	14	10	20

[a] Column totals do not equal 100% because of inclusion of carabid species subtotals and exclusion of less common taxa.

cluding the sum of adult carabids), PROC CORR was used to test for the presence of any significant relationships ($P < 0.05$, one-tailed test). If two or more predator groups were positively related to percent predation, the group with the highest correlation coefficient (r) was selected. This approach attempts to link any whole plot or split-plot effects on predation to a predator group, although selection of only one group for each contrast likely excludes some taxa contributing to predation. However, this decision was made to prevent entry of variables with spurious partial correlations to percent predation. That is, the presence of clear significant relationships was valued over higher coefficients of determination (R^2) that might be achieved using forward selection or all-possible-regressions procedures (Neter et al. 1996).

Results

Predator Community Composition and Abundance. Arthropod collections from pitfall traps during 2004–2005 were mostly comprised of three family- or order-level groups: carabid beetle adults, harvestmen (Arachnida: Opiliones), and spiders (Arachnida: Araneae). However, the distribution of predator taxa differed among the main plots and between years (Table 1). More ground beetles were collected in corn and soybean compared with forage whole plots, particularly in 2004. Also, it seemed the relative abundance of two carabid species, *Poecilus chalcites* (Say) and *Scarites quadriceps* Chaudior, declined in corn and soybean plots, whereas the number of *Harpalus pensylvanicus* (DeGeer) and harvestmen increased in 2005.

The split-plot analyses of total predator abundance in 2004 show total predator abundance was influenced by the living mulches during all four sample periods. The number of predators collected differed between forage whole plots and the annual crops (combined) during one sample period (September) and no crop × mulch interactions were found. Conversely, in 2005, living mulches only seemed to impact predator levels during June, but significant crop × mulch interactions were found in July, August, and September (Table 2). Contrasts confirm tests on main effects (i.e., crop and mulch) for 2004, showing significant increases in predator abundance for the living mulches in both corn and soybean during all four sample periods (Fig. 1). However, results of contrasts diverge from main effects testing for 2005, particularly for sample periods where crop × mulch interactions were detected; contrasts show living mulches increased predator abundance in August (corn) and September (soybean), whereas more predators were collected in alfalfa and kura clover in corn and soybean compared with forage whole plots in July (Fig. 2).

Feeding on Sentinel Prey. Including all sample periods, ~2% of the 2,560 European corn borer pupae used as sentinel prey each year were categorized as missing (2004, n = 53; 2005, n = 33), whereas the percentage preyed on averaged 55% (2004, n = 1,363; 2005, n = 1,432). In 2004, the mixed-model indicated feeding on pupae was affected by living mulches in June, July, and August, whereas predation differed between the forage whole plots and the annual crops (combined) for all sample periods. In 2005, the same effects of living mulches (August) and annual crops

Table 2. Split-plot analyses of predator abundance by sample period, 2004–2005

Year	Effect	Sample period							
		June		July		Aug.		Sept.	
		F[a]	P	F	P	F	P	F	P
2004	Crop	1.22	0.360	1.67	0.266	0.01	0.989	5.67	0.042
	Mulch	14.77	<0.001	7.08	0.007	4.87	0.024	9.33	0.002
	Interaction	0.58	0.635	1.64	0.223	0.05	0.985	0.86	0.485
2005	Crop	0.94	0.442	4.52	0.064	1.99	0.218	0.93	0.445
	Mulch	4.22	0.035	2.55	0.111	2.83	0.090	1.21	0.326
	Interaction	1.64	0.222	3.68	0.036	3.40	0.046	4.82	0.015

[a] Degrees of freedom for F-tests: crop: 2, 6; mulch: 2, 15; crop × mulch: 3, 15

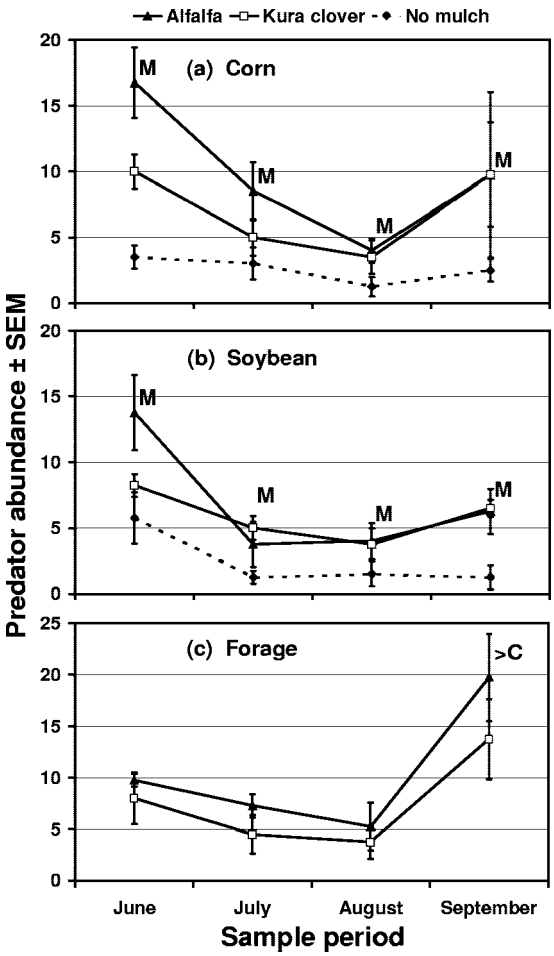

Fig. 1. Predator abundance (mean per plot ± SEM) in (a) corn, (b) soybean, and (c) forage whole plots from June through September 2004. M, significant contrasts between combined mulch treatments and control for corn or soybean plots; C, differences for combined mulch treatments in forage versus combined mulch treatments in corn and soybean. Untransformed data presented for clarity.

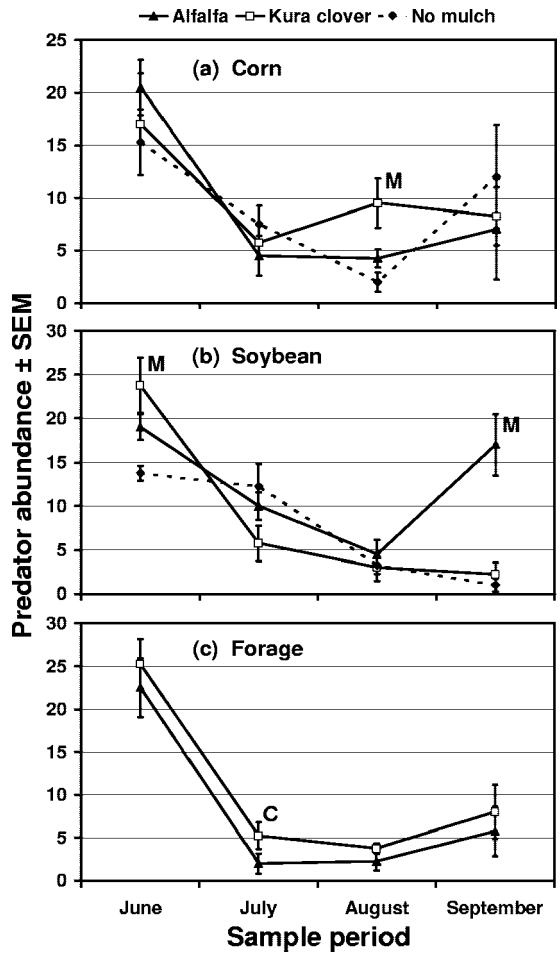

Fig. 2. Predator abundance (mean per plot ± SEM) in (a) corn, (b) soybean, and (c) forage whole plots from June through September 2005. M, significant contrasts between combined mulch treatments and control for corn or soybean plots; C, differences for combined mulch treatments in forage versus combined mulch treatments in corn and soybean. Untransformed data presented for clarity.

(July, September) on predation were detected less frequently, although significant crop × mulch interactions were present for the August and September sample periods (Table 3). Contrasts in 2004 support the analysis of main effects, although, in soybean, increased predation in the living mulches was only indicated in July (Fig. 3). Contrasts for 2005 predation data clarify the effects of the living mulches for periods where crop × mulch interactions were present, indicating the living mulches enhanced predation in corn during August and September (Fig. 4).

Relationship of Predator Abundance to Percent Predation. Among the taxa collected in pitfall traps, only carabid beetles seemed significantly related to pupal predation (Table 4). For the six contrasts indicating an effect of living mulches on predation in 2004–2005, five positive correlations with a common carabid species or all carabids collectively explained 37–58% of the variation in untransformed data on consumption of sentinel prey. Correlations that may explain differences in predation between the living mulch split-plots in the annual crops and the forage plots were found for only three of six contrasts, explaining 19–40% of the variation in predation of European corn borer pupae.

Discussion

The addition of alfalfa and kura clover living mulches into corn and soybean increased both the abundance of ground-dwelling predators (Figs. 1 and 2; Table 2) and the consumption of lepidopteran pupae used as sentinel prey compared with a no-mulch control (Figs. 3 and 4; Table 3). When detected, the effects of living mulches on predator abundance or percent predation were often large (50–100% differ-

Table 3. Split-plot analyses of predation on sentinel prey by sample period, 2004–2005

Year	Factor	Sample period							
		June		July		Aug.		Sept.	
		F^a	P	F	P	F	P	F	P
2004	Crop	9.18	0.015	10.35	0.011	6.39	0.033	78.07	<0.001
	Mulch	9.07	0.003	10.82	0.001	4.22	0.035	0.28	0.762
	Interaction	0.90	0.463	1.26	0.324	0.87	0.478	1.13	0.369
2005	Crop	0.55	0.604	17.65	0.003	1.99	0.218	41.70	<0.001
	Mulch	2.84	0.090	1.93	0.180	5.94	0.013	3.32	0.064
	Interaction	0.54	0.665	1.19	0.346	14.71	<0.001	4.85	0.015

[a] Degrees of freedom for F-tests: crop, 2,6; mulch, 2,15; crop × mulch, 3,15.

ence), implying both statistical and biological significance. Furthermore, positive correlations between the abundance of carabid beetles and predation of European corn borer pupae suggest alfalfa and kura clover may improve biological control of pests near the soil surface (Table 4).

Effects of annual crops on the living mulches also were detected by using contrasts with alfalfa and kura

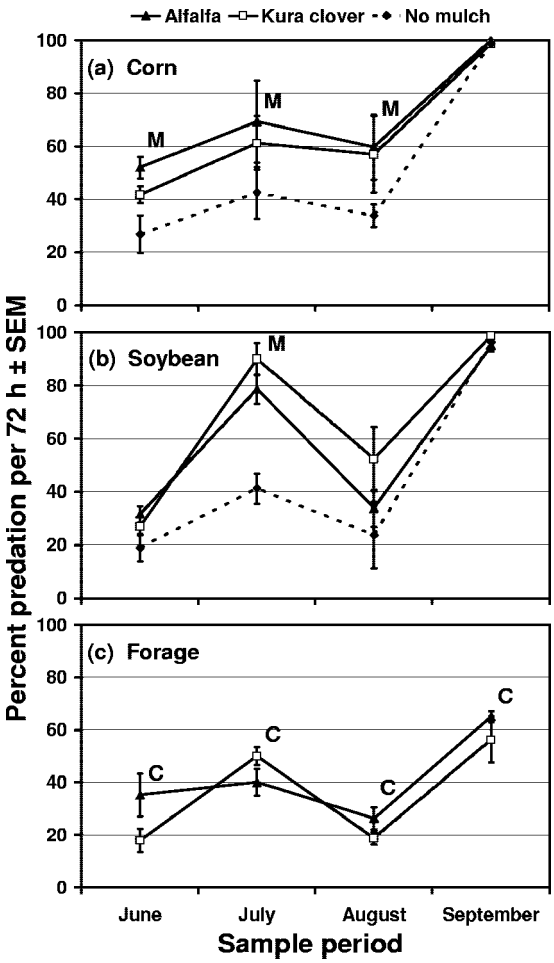

Fig. 3. Percent of European corn borer pupae fed upon (mean per plot ± SEM) in (a) corn, (b) soybean, and (c) forage whole plots from June through September 2004. M, significant contrasts between combined mulch treatments and control for corn or soybean plots; C, differences for combined mulch treatments in forage versus combined mulch treatments in corn and soybean.

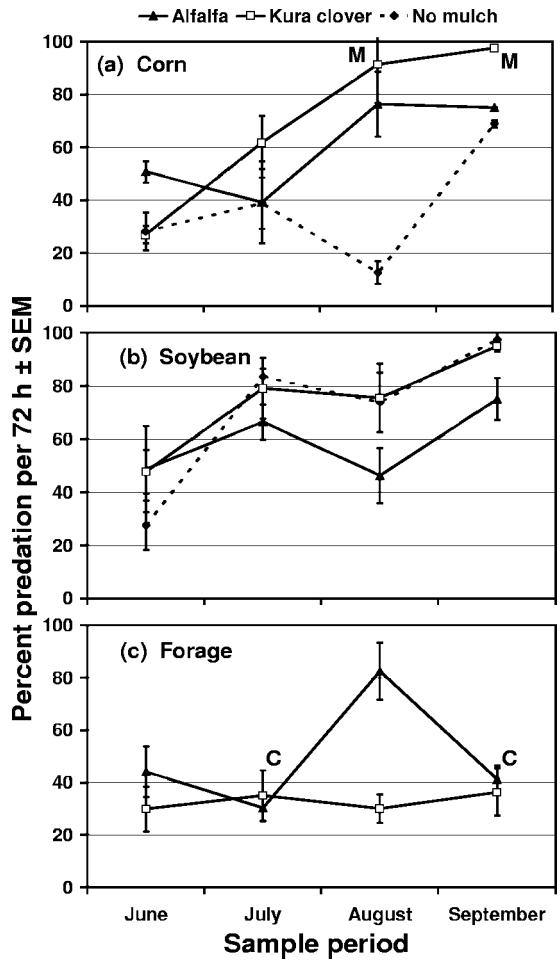

Fig. 4. Percent of European corn borer pupae fed upon (mean per plot ± SEM) in (a) corn, (b) soybean, and (c) forage whole plots from June through September 2005. M, significant contrasts between combined mulch treatments and control for corn or soybean plots; C, differences for combined mulch treatments in forage versus combined mulch treatments in corn and soybean.

Table 4. Significant correlations between predation and predator abundance, 2004–2005

Year	Sample period	Effect	Predator group[a]	r^2	P^b
2004	June	Mulches in corn	*P. chalcites*	0.40	0.014
	June	Crop in mulches	*S. quadriceps*	0.26	0.005
	July	Mulches in soybean	Carabid adults	0.42	0.011
	Aug.	Mulches in corn	*H. pensylvanicus*	0.37	0.018
	Sept.	Crop in mulches	*P. permundus*	0.40	<0.001
2005	July	Crop in mulches	*S. quadriceps*	0.19	0.018
	Aug.	Mulches in corn	Carabid adults	0.58	0.002
	Sept.	Mulches in corn	*H. pensylvanicus*	0.37	0.019

[a] Predator abundance data $\log_{10}(x + 1)$ transformed.
[b] *P* values are for correlation coefficient (one-tailed test).

clover in the forage whole plots. Sentinel prey consumption in the corn and soybean crops with mulches was significantly higher than in forage-only plots for six of eight contrasts in 2004–2005 (Figs. 3 and 4). Because living mulch studies do not generally include mulch treatments grown without a main crop, this positive complementary effect of annual crops on predation may not have previously been observed or reported.

Composition of the natural enemy community also may be more important than total predator abundance in some cases. For example, the increased predation in corn and soybean whole plots seemed unrelated to overall predator abundance; in only one of eight contrasts were more predators found in the living mulch split-plots in corn and soybean compared with both mulches in the forage plots (Figs. 1 and 2). However, higher predation was observed in the annual crops for six of the same eight sample periods (Figs. 3 and 4). A greater relative abundance of common carabid species in corn and soybean plots (Table 1) may explain the higher percent predation observed in these plots.

Differences between 2004 and 2005 include changes in carabid species composition (Table 1) and an apparent decline in the benefits produced by living mulches in corn and soybean plots (Figs. 3 and 4). Specifically, fewer *Poecilus chalcites* (2004, $n = 69$; 2005, $n = 18$) and *Scarites quadriceps* (2004, $n = 70$; 2005, $n = 49$) were trapped in corn and soybean in 2005. Because these species were collected mostly during June (97% of *S. quadriceps*) or June and July (84% of *P. chalcites*), it seems plausible that their relative scarcity in 2005 could have prevented living mulches from augmenting predation during the early sample periods (Table 4; Fig. 4). Conversely, the number of *Harpalus pensylvanicus* increased dramatically (2004, $n = 40$; 2005, $n = 195$) between years. Although *H. pensylvanicus* is sometimes characterized as herbivorous or spermophagous, significant positive correlations with pupal feeding (Table 4) and other reports of predation by *H. pensylvanicus* (Kirk 1973, Riddick and Mills 1994, Losey and Denno 1998) suggest it has some value for pest suppression and might best be considered an omnivore. The primary difference in crop management in 2005 was a long delay in glyphosate applications to suppress living mulches in corn and soybean plots, which resulted in increased competition between the mulches and annual crops (J.W.S., unpublished data). Although not conclusive, the importance of vegetation structure to predator community composition and performance (Booij and Noorlander 1992, Cárcamo and Spence 1994) suggests the unchecked early growth of the living mulches could have produced both of the observed year-to-year differences.

Correlations between the abundance of adult carabids and percent predation are insufficient to prove a cause-and-effect relationship per se, but direct observation of predation events indicate that carabid beetle density and predation on lepidopteran larvae (including *O. nubilalis*) are strongly related (Brust et al. 1986). Furthermore, the nature of this study supports the conclusion that increases in predator abundance and sentinel prey consumption were directly related. First, by measuring predation instead of herbivore abundance, treatment differences cannot be attributed to living mulches impairing herbivore colonization. Additionally, the controlled and consistent density of corn borer pupae in treatments reduces the potential confounding effects of density dependence.

Frequent associations between ground beetles and predation in this and other studies (O'Neal et al. 2005) sometimes emphasize carabids to the near exclusion of other arthropods. However, variation not explained by simple correlations suggests that predation by other groups could have been considerable, particularly in the forage crop where ground beetles were less common. Spiders are generally accepted as playing a complementary role in agricultural pest suppression, and observations by Brust et al. (1986) and Newton and Yeargan (2001) also indicate harvestmen may be important ground-dwelling predators for lepidopteran pests. Other taxa known to be common but not collected frequently in pitfall traps (e.g., ants; Brust et al. 1986) might also contribute to suppression of pests near ground level.

While living mulches alone are unlikely to provide adequate pest suppression, the initial results for a rotation incorporating corn and soybean crops agree with previous studies showing the potential benefits of living ground covers to pest management (Costello 1994, Bigler et al. 1995a, b, Costello and Altieri 1995, Vidal 1997, Brandsæter et al. 1998, Hooks et al. 1998, Hooks and Johnson 2004, Frank and Liburd 2005). The ability to detect the effects of living mulch treatments in relatively small plots also suggests that more en-

couraging results are possible in larger trials (Prasifka et al. 2005). Aside from increasing the scale of study, broader research on the impact of living mulches on pest management (e.g., possible effects on foliar pests and natural enemies, weed seed predation) in corn and soybean is needed. Although the direct effects of living mulches on soil quality and crop yields are likely most important, the potential benefit to pest management is another factor to consider for systems into which living mulches can be integrated.

Acknowledgments

This research was a joint contribution from the USDA Agricultural Research Service and the Iowa Agriculture and Home Economics Experiment Station, Ames (Project 3543). This article reports the results of research only. Field assistance by E. Patrin, A. Veine, K. Johnson, P. O'Neal, T. Horton, and E. Mauch is greatly appreciated. Assistance in identification of carabids species by K. Larson is also acknowledged. Earlier versions of this manuscript were improved by the comments of S. Fleischer, D. Landis, P. Prasifka, and T. Sappington.

References Cited

Affeldt, R. P., K. A. Albrecht, C. M. Boerboom, and E. J. Bures. 2004. Integrating herbicide-resistant corn technology in a kura clover living mulch system. Agron. J. 96: 247–251.

Andow, D. A. 1991. Vegetational diversity and arthropod population response. Annu. Rev. Entomol. 36: 561–586.

Bigler, F., M. Walburger, and G. Frei. 1995a. Vier maisanbauverfahren 1990 bis 1993: Inseckten und spinnen als nützlinge. Agraforschung 2: 383–386.

Bigler, F., M. Walburger, and G. Frei. 1995b. Vier maisanbauverfahren 1990 bis 1993: Krankheiten und schadlinge. Agraforschung 2: 380–382.

Blackmer, A. M., D. Pottker, M. E. Cerrato, and J. Webb. 1989. Correlations between soil nitrate concentrations in late spring and corn yield in Iowa. J. Prod. Agric. 2: 103–109.

Booij, C. J., and J. Noorlander 1992. Farming systems and insect predators. Agric. Ecosyst. Environ. 40: 125–135.

Brandsæter, L. O., J. Netland, and R. Meadow. 1998. Yields, weeds, pests and soil nitrogen in a white cabbage living mulch system. Biol. Agric. Hortic. 16: 291–309.

Brophy, L. S., G. H. Heichel, and M. P. Russelle. 1987. Nitrogen transfer from forage legumes to grass in a systematic planting design. Crop Sci. 27: 753–758.

Brust, G. E., B. R. Stinner, and D. A. McCartney. 1986. Predator activity and predation in corn agroecosystems. Environ. Entomol. 15: 1017–1021.

Cárcamo, H. A., and J. R. Spence 1994. Crop type effects on the activity and distribution of ground beetles (Coleoptera: Carabidae). Environ. Entomol. 23: 684–692.

Costello, M. J. 1994. Broccoli growth, yield and level of aphid infestation in leguminous living mulches. Biol. Agric. Hortic. 10: 207–222.

Costello, M. J. 1995. Spectral reflectance from a broccoli crop with vegetation or soil as background—influence on immigration by *Brevicoryne brassicae* and *Myzus persicae.* Entomol. Exp. Appl. 75: 109–118.

Costello, M. J., and M. A. Altieri 1995. Abundance, growth-rate and parasitism of *Brevicoryne brassicae* and *Myzus persicae* (Homoptera: Aphididae) on broccoli grown in living mulches. Agric. Ecosyst. Environ. 52: 187–196.

Duiker, S. W., and N. L. Hartwig 2004. Living mulches of legumes in imidazolinone-resistant corn. Agron. J. 96: 1021–1028.

Echtenkamp, G. W., and R. S. Moomaw 1989. No-till corn production in a living mulch system. Weed Technol. 3: 261–266.

Enache, A. J., and R. D. Ilnicki 1990. Weed-control by subterranean clover (*Trifolium subterraneum*) used as a living mulch. Weed Technol. 4: 534–538.

Finch, S., and M. Kienegger. 1997. A behavioural study to help clarify how undersowing with clover affects host-plant selection by pest insects of brassica crops. Entomol. Exp. Appl. 84: 165–172.

Frank, D. L., and O. E. Liburd 2005. Effects of living and synthetic mulch on the population dynamics of whiteflies and aphids, their associated natural enemies, and insect-transmitted plant diseases in zucchini. Environ. Entomol. 34: 857–865.

Hartwig, N. L., and H. U. Ammon 2002. 50th anniversary—invited article: Cover crops and living mulches. Weed Sci. 50: 688–699.

Holling, C. S. 1961. Principles of insect predation. Annu. Rev. Entomol. 6: 163–182.

Hooks, C. R., and M. W. Johnson 2004. Using undersown clovers as living mulches: effects on yields, lepidopterous pest infestations, and spider densities in a Hawaiian broccoli agroecosystem. Int. J. Pest Manag. 50: 115–120.

Hooks, C. R., H. R. Valenzuela, and J. Defrank. 1998. Incidence of pests and arthropod natural enemies in zucchini grown with living mulches. Agric. Ecosyst. Environ. 69: 217–231.

Hummel, R. L., J. F. Walgenbach, G. D. Hoyt, and G. G. Kennedy. 2002. Effects of production system on vegetable arthropods and their natural enemies. Agric. Ecosyst. Environ. 93: 165–176.

Ilnicki, R. D., and A. J. Enache 1992. Subterranean clover living mulch: an alternative method of weed control. Agric. Ecosyst. Environ. 40: 249–264.

Kirk, V. M. 1973. Biology of a ground beetle, *Harpalus pensylvanicus.* Ann. Entomol. Soc. Am. 66: 513–517.

Losey, J. E., and R. F. Denno. 1998. Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology 79: 2143–2152.

Mallarino, A. P., W. F. Wedin, C. H. Perdomo, R. S. Goyenola, and C. P. West. 1990. Nitrogen transfer from white clover, red clover, and birdsfoot trefoil to associated grass. Agron. J. 82: 790–795.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models, 3rd ed. McGraw-Hill, Boston, MA.

Newton, B. L., and K. V. Yeargan 2001. Predation of *Helicoverpa zea* (Lepidoptera: Noctuidae) eggs and first instars by *Phalangium opilio* (Opiliones: Phalangiidae). J. Kans. Entomol. Soc. 74: 199–204.

O'Neal, M. E., E. L. Zontek, Z. Szendrei, D. A. Landis, and R. Isaacs. 2005. Ground predator abundance affects prey removal in highbush blueberry (*Vaccinium corymbosum*) fields and can be altered by aisle ground covers. BioControl 50: 205–222.

Prasifka, J. R., R. L. Hellmich, G. P. Dively, and L. C. Lewis. 2005. Assessing the effects of pest management on nontarget arthropods: the influence of plot size and isolation. Environ. Entomol. 34: 1181–1192.

Riddick, E. W., and N. J. Mills. 1994. Potential of adult carabids (Coleoptera: Carabidae) as predators of 5th-instar codling moth (Lepidoptera: Tortricidae) in apple orchards in California. Environ. Entomol. 23: 1338–1345.

Risch, S. J., D. Andow, and M. A. Altieri. 1983. Agroecosystem diversity and pest control - data, tentative conclusions, and new research directions. Environ. Entomol. 12: 625–629.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats—fauna of collards (*Brassica oleracea*). Ecol. Monogr. 43: 95–120.

Russell, E. P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ. Entomol. 18: 590–599.

SAS Institute. 1999. SAS OnlineDoc, version 8. SAS Institute, Cary, NC.

Sheehan, W. 1986. Response by specialist and generalist natural enemies to agroecosystem diversification: a selective review. Environ. Entomol. 15: 456–461.

Tharp, B. E., and J. J. Kells. 2001. Delayed burndown in no-tillage glyphosate-resistant corn (*Zea mays*) planted into soybean (*Glycine max*) residue and a wheat (*Triticum aestivum*) cover crop. Weed Technol. 15: 467–473.

Vidal, S. 1997. Factors influencing the population dynamics of *Brevicoryne brassicae* in undersown Brussels sprouts. Biol. Agric. Hortic. 15: 285–295.

Voss, R. D., J. E. Sawyer, A. P. Mallarino, and R. Killorn 2002. General guide for crop nutrient recommendations in Iowa. Iowa State University Cooperative Extension Service, Ames, IA.

Received for publication 5 May 2006; accepted 8 July 2006.